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A NEW PALEOCENE PALAEANODONT AND THE ORIGIN OF THE METACHEIROMYIDAE (MAMMALIA)

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ABSTRACT. A new genus and species of palaeanodont, *Propalaeanodon schaffi*, from the late Paleocene (late Tiffanian) Polecat Bench Formation of the Bighorn Basin, Wyoming, is the oldest and most primitive known metacheiromyid. *Propalaeanodon* foreshadows *Palaeanodon* in the reduction of its postcanine teeth. It resembles epoicotheriids in the presence of postcanines along the entire length of the horizontal ramus, and resembles the slightly older *Amelotabes*, in particular, in the retention of seven postcanines. *Propalaeanodon* thus provides additional evidence for uniting the Metacheiromyidae and the Epoicotheriidae in the suborder Palaeanodonta, and it strongly suggests that the Metacheiromyidae evolved from the Epoicotheriidae, probably during the Tiffanian.

Two humeri from the same stratigraphic level as the holotype are tentatively referred to *Propalaeanodon*. They possess specializations typical of Eocene palaeanodonts, including a prominent deltopectoral crest and a large supinator crest. These features indicate that *Propalaeanodon* was, already in the late Tiffanian, a highly specialized fossorial animal.

The systematic position of the Palaeanodonta is uncertain. They have been considered to be related to the orders Xenarthra or Pholidota or both by all recent students and, indeed, they are the only known fossil group that evolved specializations similar to those in these two orders. Although it is possible that palaeanodonts were an early radiation of probably myrmecophagous, fossorial mammals merely convergent to these orders, the evidence now available enhances the probability that the three groups share a special relationship.

INTRODUCTION

The edentate-like members of the rare mammalian suborder Palaeanodonta have long been considered early relatives of the Xenarthra, the Pholidota, or both. As now known, they are restricted to the earlier Tertiary of western North America. Palaeanodonts are classified in two families, the Epoicotheriidae and the

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Metacheiromyidae. To date, nine genera and fifteen species have been recognized, several of which were described quite recently (West, 1973; Rose et al., 1977; Rose, 1978). They range in age from Tiffanian (late Paleocene) to Orellan (middle Oligocene).

Recently the dentary of a primitive new palaeanodont was discovered by Charles Schaff, Museum of Comparative Zoology, in late Tiffanian rocks in the northern Bighorn Basin, Wyoming. The oldest and most primitive metacheiromyid, it sheds new light on the origin of this peculiar family and further documents the unity of the Palaeanodonta. Two palaeanodont humeri, collected much earlier from the same stratigraphic interval, probably represent the same new species.

Abbreviations of institutional names cited herein are as follows:

AC Pratt Museum, Amherst College, Amherst, Massachusetts.

AMNH American Museum of Natural History, New York.

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

PU Princeton University Museum, Princeton, New Jersey.

UM University of Michigan Museum of Paleontology, Ann Arbor, Michigan.

SYSTEMATIC PALEONTOLOGY

Suborder PALAEANODONTA Matthew, 1918
Family METACHEIROMYIDAE Wortman, 1903
PROPALAEANODON, gen. nov.

Type species. Propalaeanodon schaffi, sp. nov.

Included species. Type only.

Distribution. Late Paleocene (late Tiffanian) oι the Bighorn Basin, Wyoming.

Diagnosis. Only metacheiromyid with seven postcanine teeth that extend to the back of the horizontal ramus. All postcanines single-rooted except P_4, which is two-rooted. Postcanines small, peglike, separated by short diastemata, and with rounded crowns, in these features resembling *Palaeanodon;* but crowns higher and more pointed than in *Palaeanodon*. Dentary slender, slightly smaller than in *Palaeanodon ignavus;* deepest beneath first postcanine (P_1), shallowest beneath last postcanine (M_3), as in *Palaeanodon*. Medial buttress prominent but less so than in *Palaeanodon*.

Etymology. In allusion to its resemblance to, lower stratigraphic level than, and probable relationship to *Palaeanodon.*

PROPALAEANODON SCHAFFI, sp. nov.
Fig. 1A and B, 2A, and 3B

Holotype: MCZ 20122, left dentary with P_{2-3}, alveoli for P_1, P_4, M_{1-3}, and posterior margin of canine alveolus.

Hypodigm. Holotype and tentatively PU nos. 13928, 13929.

Horizon and Locality. Latest Paleocene (late Tiffanian), "Silver Coulee beds" of Polecat Bench Formation (of Jepsen, 1940), Jepsen Valley Quarry, NW¼, Sec. 27, T.57N., R.100W., Park County, Wyoming.

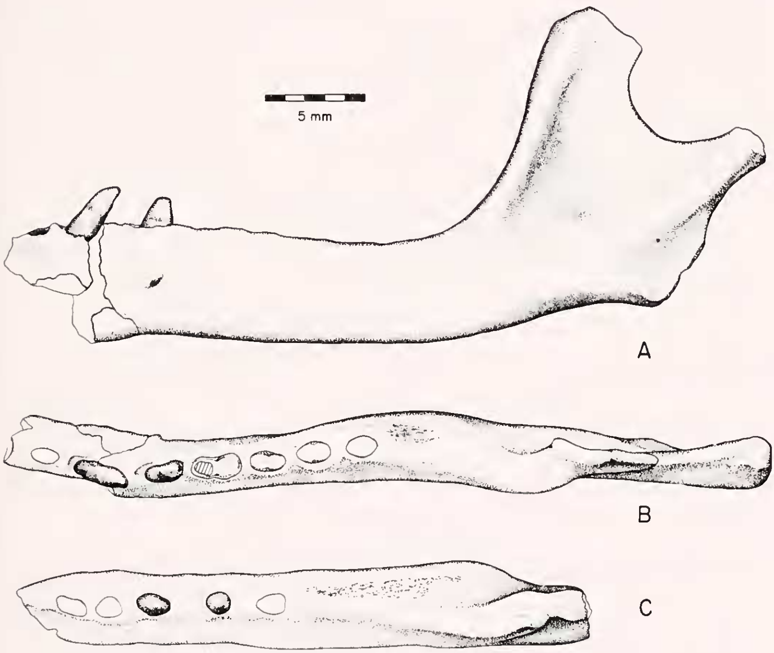

Figure 1. Lateral (A) and dorsal (B) views of holotype of *Propalaeanodon schaffi,* MCZ 20122, left dentary with second and third postcanines (P_{2-3}). Dorsal view of left dentary of *Palaeanodon* sp. (C), showing extended edentulous part of ramus behind fifth postcanine; reconstructed from UM 63611 and 66243.

Figure 2. Medial views of left dentaries of palaeanodonts. (A) *Propalaeanodon schaffi*, holotype, MCZ 20122. (B) *Palaeanodon* sp., reconstruction based on UM 63611 and 66243. (C) *Amelotabes simpsoni*, holotype, PU 14855 (right dentary, reversed).

Diagnosis. Only known species of the genus; measurements in Table 1.

Etymology. For Charles R. Schaff, expert collector and preparator, who discovered the holotype.

Description. Only two teeth are preserved in the holotype, although the dentary is nearly complete and provides much information about the mandibular morphology of *Propalaeanodon schaffi*. The horizontal ramus is intact as far forward as the posterior margin of the canine alveolus. This alveolar margin reveals that the canine was large, as in other palaeanodonts, and its

root robust, a feature also indicated by thickening of the dentary anteriorly.

The dentary contained seven postcanine teeth, presumably four premolars and three molars, which were greatly modified from the primitive eutherian condition. Seven is a greater number of teeth than in any other metacheiromyid, indeed more than in any other palaeanodont except *Amelotabes,* which also has seven (Rose, 1978). *Alocodontulum,* in which the lower dentition is unknown, has seven upper postcanines (Rose et al., 1977, 1978), and thus probably had seven lowers as well. The postcanines of *Propalaeanodon* occur along the entire length of the horizontal ramus, as in

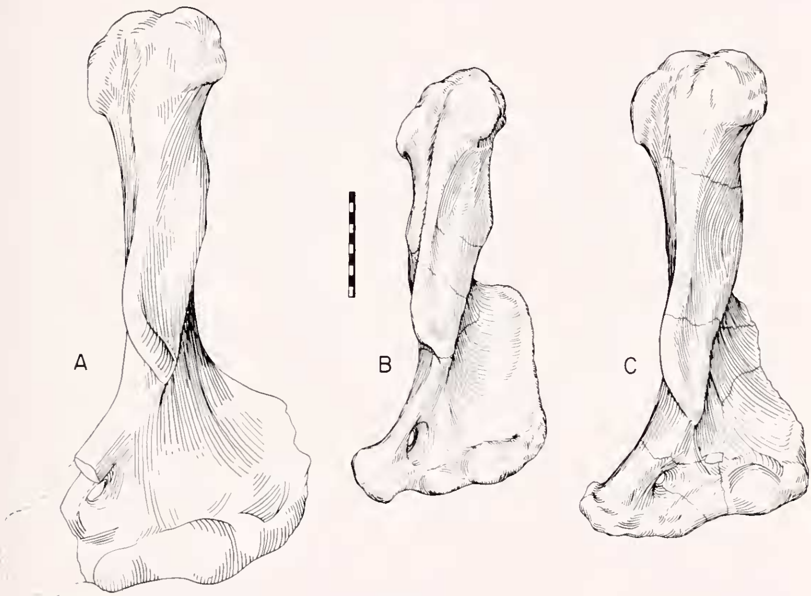

Figure 3. Left humeri of palaeanodonts. Scale is 10 mm. (A) Early Eocene metacheiromyid *Palaeanodon ignavus,* based on AMNH 15088 and 16832; after Matthew (1918), but with corrected orientation of proximal end. (B) ?*Propalaeanodon schaffi,* PU 13928. (C) Early Eocene epoicotheriid *Pentapassalus woodi,* part of holotype, AC 2766. Note that this species is referable to *Pentapassalus* (Rose, 1978), not to *Palaeanodon* (Guthrie, 1967; Emry, 1970). The supinator crests in (A) and (C) are incomplete and have not been reconstructed because of the variable development of this crest in different taxa of palaeanodonts; they were in any case larger than depicted.

TABLE 1

Dimensions of the holotype of *Propalaeanodon schaffi*, MCZ 20122. (Measurements are in mm to nearest .05 mm)

	Length	Breadth
P_1 alveolus	1.35	0.85
P_2 alveolus	damaged	
P_2 crown	1.25	1.00
P_3 alveolus	2.40	1.15
P_3 crown	1.80	1.10
P_4 alveolus	2.80	1.10
M_1 alveolus	2.00	1.15
M_2 alveolus	2.00	1.15
M_3 alveolus	1.60	1.00
P_1-M_3	17.10 (approx.)	

Depth of mandible, lingually at P_1: 6.10 (approx.)
Depth of mandible, lingually at M_3: 4.80

epoicotheriids but not in later metacheiromyids, in which the back of the horizontal ramus is edentulous. All teeth in *Propalaeanodon* are single-rooted except P_4, which has two roots (probably a primitive feature). Judging from the alveoli, M_1 and M_2, and possibly P_3, had single roots that were faintly bilobate. The roots of all postcanines were tapered and closed, as in *Palaeanodon*. The epoicotheriids *Amelotabes* (Fig. 2C) and *Tubulodon* are similar in having a two-rooted P_4, but in these taxa several other postcanines are also two-rooted. In *Pentapassalus* M_1 has a bilobate root but P_4 is single-rooted (Gazin, 1952). The postcanines in *Palaeanodon* are all single-rooted (Fig, 1C, 2B).

The crowns of P_2 and P_3 are preserved. P_2 has become dislodged from its alveolus as a result of damage to the front of the jaw and appears higher than P_3. Both teeth are peglike with rounded crowns apparently devoid of enamel. In these characters they closely resemble the postcanines of *Palaeanodon* (Fig. 1C, 2B and Rose, 1978), although they are slightly larger, particularly longer, higher crowned, and less rounded. As in *Palaeanodon* they show no cusp pattern on the crowns, nor is there any evidence of direct occlusion with the upper teeth. Occlusal wear is discernible in molars and even in premolars of some epoicotheriids. The alveolus of P_4 indicates

that it was the largest cheek tooth, a feature in common with *Amelotabes* but in contrast to *Palaeanodon*. There is a slight size reduction from P_4 to M_3.

All postcanines are separated by short diastemata. At the alveolar margin, the alveoli of P_{2-4} slightly exceed the size of the roots they contain; this probably obtained for the molars as well. These traits are characteristic also of *Palaeanodon*, some advanced epoicotheriids, and many toothed xenarthrans.

The ascending ramus and condyle of *Propalaeanodon* resemble those of *Pentapassalus pearcei* and *Metacheiromys tatusia* (Gazin, 1952; Simpson, 1931). The coronoid process is slightly smaller than in contemporary proteutherians (*sensu* Butler, 1972) and rises at an angle of about 110° to the ventral border of the mandible. The condyle, which is narrower transversely than in most toothed xenarthrans and contemporary proteutherians, is situated relatively low but above the level of the tooth row. Its convex articular surface is directed dorsally and backward, as in *P. pearcei*. The mandibular foramen is also relatively low, being situated on the posterior projection of the tooth row. The internal mandibular groove extends from just anterior to this foramen to a point beneath M_1.

As in all metacheiromyids, there is a prominent medial buttress, forming anteriorly a low, narrow ridge lingual to the molars. The dorsal surface of the buttress is roughened, particularly behind M_3. On the external surface of the mandible the masseteric fossa, though rather poorly defined, is deeper than in most other palaeanodonts. The fossa is bounded in front by a crest formed by the thickened anterior border of the coronoid. A more rounded ridge running forward from the condyle forms its lower limit. The horizontal ramus is rather slender and shallow, deeper in front than in back, as in *Palaeanodon*. A small mental foramen is present beneath P_3.

Two palaeanodont humeri from Princeton Quarry are probably referable to *Propalaeanodon schaffi* (Princeton Quarry is about ½ mile northwest of Jepsen Valley Quarry and at about the same stratigraphic level). They are the only other palaeanodont specimens from the same stratigraphic interval as the holotype. PU 13928, a complete left humerus (Fig. 3B), and PU 13929, a distal end of a left humerus, are of appropriate size for *Propalaeanodon*. They are smaller than the humeri of *Palaeanodon ignavus* (Fig. 3A) and *Pentapassalus woodi* (Fig. 3C and Rose, 1978) and slightly larger

TABLE 2

Dimensions (mm.) of humeri in certain palaeanodonts.
(Known humeri of *Palaeanodon* are too incomplete to allow accurate measurements.)

	?*Propalaeanodon schaffi*, PU 13928	*Metacheiromys dasypus*, AM 11718	*Pentapassalus pearcei* (from Gazin, 1952)	*Pentapassalus woodi*, AC 2766
length	39.3	74.0	37.0	47.1
length of deltopectoral crest (from proximal end of greater tuberosity)	26.3	54.7	28.0	35.5
length of supinator crest (from distal end of humerus)	19.7	38.8	22.0	20.8a
greatest transverse breadth of distal end of humerus	19.8	34.0	21.7	22.6

a = approximate

than the humeri of *Pentapassalus pearcei* (Gazin, 1952). However, all these specimens are essentially similar in structure (see Table 2 for comparative dimensions).

The deltopectoral crest is broad and well developed in PU 13928. It may be relatively slightly longer than in *Palaeanodon*, but this is not certain because the known humeri of the latter are fragmentary and poorly preserved (AMNH nos. 15088, 16831, 16832). The crest is relatively shorter than in *Pentapassalus* and *Metacheiromys* (see Simpson, 1931: 340–342). Its distal end is developed into an anteromedially directed prominence for the insertion of the pectoralis major. Proximolaterally the crest gives rise to a low process for the insertion of the deltoid. A less well-defined crest extends distally from the lesser tuberosity almost to the entepicondylar foramen and bears a small teres tubercle midway along the shaft, on which the teres major inserted, as in *Metacheiromys dasypus* (Simpson, 1931).

The supinator crest is somewhat smaller than in *Pentapassalus pearcei* and *Metacheiromys dasypus* and lacks the hooklike, dorsally projecting flange characteristic of the latter two species.

Nonetheless, this crest is very large and served as the site of origin for the powerful supinator muscle and carpal extensors, and probably the brachioradialis. The median epicondyle (the point of origin of the pronator teres and the carpal flexors) is also large, although smaller than in *Palaeanodon* and *Pentapassalus*. These features of the humerus indicate an animal highly adapted for fossorial habits (Reed, 1954; Hildebrand, 1974). Although the development of the deltopectoral crest in palaeanodonts is (as Emry, 1970, asserts) more like that of manids than of armadillos, the development of the supinator crest is more extreme, even in PU 13928, than in either manids or xenarthrans.

DISCUSSION

Propalaeanodon is the second known Paleocene palaeanodont and the only known Paleocene metacheiromyid. A number of resemblances to epoicotheriids were described above — e.g., seven postcanines, teeth present at the back of the horizontal ramus, two-rooted P_4 — but these are primitive features of palaeanodonts. *Propalaeanodon* resembles *Palaeanodon* (Fig. 1 and 2) in the manner of reduction of its postcanines to peglike teeth (all but one single-rooted) with rounded crowns that apparently lack enamel. Like *Palaeanodon,* its postcanine teeth are housed in tapered alveoli that are larger than the roots and separated by diastemata. Although some of these features also evolved in advanced epoicotheriids (e.g., Bridgerian *Tetrapassalus mckennai,* Chadronian-?Orellan *Xenocranium pileorivale;* Simpson, 1959; Colbert, 1942), the total suite of features evolved much earlier in the metacheiromyids. Thus when metacheiromyids had already achieved these traits, contemporary epoicotheriids, as now understood, retained relatively unreduced teeth with enamel and with very short or no diastemata between them. *Tetrapassalus* and *Xenocranium* are more specialized than *Propalaeanodon* in having fewer teeth and a shortened dentary, but they are more primitive (and typically epoicotheriid) in showing occlusal wear on the teeth.

As metacheiromyids reduced the number of postcanine teeth, they retained a long dentary, hence leaving the back of the horizontal ramus edentulous. The trend in the Epoicotheriidae was toward shortening the dentary as teeth were lost. The antiquity and primitive grade of *Propalaeanodon* results in resemblances to both

metacheiromyids and certain epoicotheriids and highlights the extent of parallelism that has occurred within the Palaeanodonta.

Propalaeanodon is one of those rare fossils that is morphologically intermediate between two well defined families, and it strengthens the alliance of the Epoicotheriidae and the Metacheiromyidae in the suborder Palaeanodonta. Because of its very early acquisition of advanced traits found also in *Palaeanodon* and its stratigraphic and geographic proximity to *Palaeanodon,* I believe *Propalaeanodon* is best regarded as a primitive metacheiromyid, probably lying in or very near the ancestry of *Palaeanodon.* Its very late Paleocene age makes derivation of the Metacheiromyidae from an epoicotheriid similar to early late Tiffanian *Amelotabes* highly probable. Moreover, the primitive aspect of *Propalaeanodon* suggests that metacheiromyids did not become distinct from epoicotheriids before the Tiffanian.

The humeri tentatively referred to *Propalaeanodon* possess specializations characteristic of fossorial mammals (see Simpson, 1931 and Rose, 1978 for additional functional interpretations). They are of interest in demonstrating that the humerus was already highly specialized in this late Paleocene palaeanodont. The deltopectoral crest is very similar to that in *Palaeanodon.* The supinator crest may have been slightly larger than in *Palaeanodon,* but no specimen of *Palaeanodon* preserves a complete supinator crest.

AFFINITIES OF THE PALAEANODONTA

Resemblances of palaeanodonts to Xenarthra and Pholidota have been enumerated by several authors (Matthew, 1918; Simpson, 1931; Emry, 1970). Two questions arise from these comparisons: To what extent are these features demonstrably synapomorphic with one or the other of these orders? To what extent do they reflect parallelism or convergence?

Detailed comparisons led Matthew (1918) to conclude that the Palaeanodonta are definitely related to the Xenarthra and probably to the Pholidota as well. He found no morphologic obstacles to direct descent of both orders from *Palaeanodon,* but for geographic and faunal reasons he deemed this origin of Xenarthra unlikely. He speculated that "early Tertiary faunas of South America . . . must be derived apparently from some late Cretacic fauna, unknown to us

but presumably inhabiting some part of North America" (Matthew, 1918: 653). Simpson (1931) detailed many characters to support alliance of the Metacheiromyidae and the Xenarthra, but he concluded that they are not so closely related to the Pholidota. Nearly four decades later, Emry (1970) critically reviewed Simpson's criteria, presenting arguments that he believed vitiated them. In Emry's view, the Metacheiromyidae were directly ancestral to the Manidae, and he included both in the order Pholidota. He rejected any special relationship between palaeanodonts and Xenarthra. Emry therefore discontinued formal recognition of the suborder Palaeanodonta, questioning whether epoicotheriid-metacheiromyid ties were really closer than metacheiromyid-manid relationship.

A primary concern of these and other authors has been that known palaeanodonts were too specialized too early in the record to be direct ancestors of xenarthrans, since contemporary and differently specialized xenarthrans were known from South America (e.g., the early Eocene dasypodid *Utaetus*). In particular, tooth reduction was regarded as "prematurely specialized." The discovery of a primitive epoicotheriid (Rose, 1978) and now a primitive metacheiromyid, both from the late Paleocene and both with much less reduced dentitions, may obviate this objection. Meager evidence attests to the presence of dasypodids in the Riochican of Patagonia (Simpson, 1948), and these are possibly contemporaneous with the Paleocene palaeanodonts. However, while the age of the Riochican is usually given as late Paleocene, its precise correlation with North American land mammal ages is uncertain (Simpson, 1978). At least part of the Riochican is considered by some authors to be younger than late Paleocene, i.e. equivalent to the Clarkforkian and early Wasatchian (e.g., Marshall et al., 1977). It is known that the teeth of early xenarthrans had enamel and developed gabled wear surfaces (Simpson, 1932). Therefore *Propalaeanodon* itself, whose postcanine teeth apparently had already lost enamel and did not develop wear facets, may have been too specialized to be directly ancestral to the Xenarthra (but not Pholidota). These objections do not apply to *Amelotabes*, and nothing now known about it precludes it from possible direct ancestry to Xenarthra or Pholidota. Some postcranial features, such as the extreme development of the supinator crest in palaeanodont humeri, are more specialized than in any known xenarthrans or pholidotans. However, some members of both groups possess an expanded, though smaller, supinator crest.

If known palaeanodonts are ancestral to either Xenarthra or Pholidota, secondary reduction of the supinator crest must have occurred. This would not be required, however, if either or both orders were derived from more primitive palaeanodonts in which the supinator crest was less developed.

Paleogeographic evidence must also be considered. There was no land connection between North and South America in the late Cretaceous or in the Paleocene (Freeland and Dietz, 1971; Malfait and Dinkelman, 1972). Therefore if palaeanodonts gave rise to xenarthrans, they could only have reached South America by rafting (Patterson and Pascual, 1972). In view of the specializations of metacheiromyids and the probability that Metacheiromyidae did not evolve before the Tiffanian, their resemblances to xenarthrans are more likely the result of convergence than of true affinity. Among known fossil forms, epoicotheriids are the most likely candidates for xenarthran ancestors, although this is probably dependent on the existence of earlier representatives than are now known. Derivation of manids from early palaeanodonts is possible and may be supported by the presence of an early manid, *Patriomanis,* in the Chadronian of North America. However, contemporary (or possibly older) manids have long been known from the Quercy Phosphorites of Europe (e.g. von Koenigswald, 1969) and a middle Eocene manid was recently reported from Messel, Germany (Storch, 1978). A direct land connection between North America and Europe existed until the end of Sparnacian (early Eocene) time (McKenna, 1972), hence it was presumably possible for manids to disperse in either direction before the middle Eocene. If manids evolved from palaeanodonts, it is most parsimonious to postulate North America as the place of origin, with subsequent dispersal to Europe.

There can be little question that palaeanodonts were the closest ecological analogues of xenarthrans and pholidotans in the early Tertiary. It may be that palaeanodonts represent an early independent radiation convergent to these orders. Evidence presented here and in other recent studies, however, strengthens the possibility of relationship among these groups. Once again it appears reasonable, as Matthew (1918: 655) wrote sixty years ago, "that there is, after all, a real affinity between the Pholidota and Xenarthra."

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REFERENCES

Butler, P. M. 1972. The problem of insectivore classification. *In* K. A. Joysey and T. S. Kemp (eds.), Studies in Vertebrate Evolution. Edinburgh: Oliver and Boyd, p. 253–265.

Colbert, E. H. 1942. An edentate from the Oligocene of Wyoming. Notulae Naturae, No. 109: 1–16.

Emry, R. J. 1970. A North American Oligocene pangolin and other additions to the Pholidota. Bull. Amer. Mus. Nat. Hist. *142:* 455–510.

Freeland, G. L., and R. S. Dietz. 1971. Plate tectonic evolution of Caribbean —Gulf of Mexico region. Nature *232:* 20–23.

Gazin, C. L. 1952. The Lower Eocene Knight Formation of western Wyoming and its mammalian faunas. Smithson. Misc. Coll. *117:* 1–82.

Guthrie, D. A. 1967. The mammalian fauna of the Lysite Member, Wind River Formation, (Early Eocene) of Wyoming. Mem. S. Calif. Acad. Sci. *5:* 1–53.

Hildebrand, M. 1974. Analysis of vertebrate structure. New York: John Wiley and Sons, 710 pp.

Jepsen, G. L. 1940. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. Part I. Proc. Am. Phil. Soc. *83:* 217–341.

Malfait, B. T., and M. G. Dinkelman. 1972. Circum—Caribbean tectonic and igneous activity and the evolution of the Caribbean plate. Geol. Soc. Amer. Bull. *83:* 251–272.

Marshall, L. G., R. Pascual, G. H. Curtis, and R. E. Drake. 1977. South American geochronology: radiometric time scale for middle to late Tertiary mammal-bearing horizons in Patagonia. Science *195:* 1325–1328.

Matthew, W. D. 1918. Part V. Insectivora (cont.), Glires, Edentata. *In* W. D. Matthew and W. Granger, A revision of the Lower Eocene Wasatch and Wind River faunas. Bull. Amer. Mus. Nat. Hist. *38:* 565–657.

McKenna, M. C. 1972. Was Europe connected directly to North America prior to the middle Eocene? Evol. Biol. *6:* 179–188.

Patterson, B., and R. Pascual. 1972. The fossil mammal fauna of South America. *In* A. Keast, F. C. Erk, and B. Glass (eds.), Evolution, Mammals, and Southern Continents. Albany: State University of New York Press, p. 247–309.

Reed, C. A. 1954. Some fossorial mammals from the Tertiary of western North America. J. Paleontol. 28: 102–111.

Rose, K. D. 1978. A new Paleocene epoicotheriid (Mammalia), with comments on the Palaeanodonta. J. Paleontol. *52:* 658–674.

Rose, K. D., T. M. Bown, and E. L. Simons. 1977. An unusual new mammal from the early Eocene of Wyoming. Postilla, No. 172: 1–10.

______. 1978. *Alocodontulum*, a new name for *Alocodon* Rose, Bown and Simons, 1977, *non* Thulborn 1973. J. Paleontol. *52:* 1162.

Simpson, G. G. 1931. *Metacheiromys* and the Edentata. Bull. Amer. Mus. Nat. Hist. *59:* 295–381.

______. 1932. Enamel on the teeth of an Eocene edentate. Amer. Mus. Novitates, No. 567: 1–4.

______. 1948. The beginning of the age of mammals in South America. Bull. Amer. Mus. Nat. Hist. *91:* 1–232.

______. 1959. A new middle Eocene edentate from Wyoming. Amer. Mus. Novitates, No. 1950: 1–8.

______. 1978. Early mammals in South America: Fact, controversy, and mystery. Proc. Am. Phil. Soc. *122:* 318–328.

Storch, G. 1978. Ein Schuppentier aus der Grube Messel—zur Paläobiologie eines mitteleozänen Maniden. Natur und Mus. *108:* 301–307.

von Koenigswald, W. 1969. Die Maniden (Pholidota, Mamm.) des europäischen Tertiärs. Mitt. Bayer. Staatssamml. Paläont. hist. Geol. *9:* 61–71.

West, R. M. 1973. An early middle Eocene epoicotheriid (Mammalia) from southwestern Wyoming. J. Paleontol. *47:* 929–931.